Intense extrapair behaviour in a semicolonial passerine does not result in extrapair fertilizations

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Sperm competition is a strong force on the evolution of mating behaviour of animals, particularly birds. In monogamous birds extrapair behaviour is one main source of variation in the reproductive success of males, which has caused the evolution of paternity guards as well as strategies by females to increase the genetic quality of their descendants. We investigated the importance of sperm competition in the reproductive behaviour of serins, *Serinus serinus*. Male serins guarded their mates and also copulated frequently, indicating that sperm competition has been an important selective force affecting their mating behaviour. Females were frequently approached and chased by extrapair males that attempted extrapair copulations. However, females refused almost every attempt by extrapair males. No extrapair paternity was detected in the population, in spite of the intense extrapair behaviour of males. This supports the view that females keep strong control over paternity, and that in this population they do not seem to obtain genetic benefits from extrapair copulations. We discuss why the presence of high levels of sexual competition may not be reflected in extrapair paternity.

Sperm competition is generally considered to involve pre- and postcopulatory competition for fertilizations between males and females with interests that can be evolutionarily conflicting (Birkhead & Møller 1998; Petrie & Kempenaers 1998). Mate guarding has been documented in many species and is particularly frequent in birds, where social monogamy predominates (Birkhead 1998; Birkhead & Møller 1992). It involves a male remaining close to his mate and following her movements, during the period when fertilization of her ova is likely. Alternative hypotheses for the close proximity of partners (Birkhead & Møller 1992) lack empirical evidence supporting them. Frequent copulation constitutes another form of paternity assurance (Birkhead et al. 1987), when ecological conditions are not ideal for mate guarding and the two tactics tend to be alternatives (Møller & Birkhead 1991, 1993; Birkhead 1998).

The finding of alternative ways of pursuing fertilizations in birds led several authors (Birkhead & Biggins 1987; Westneat et al. 1990; Birkhead & Møller 1992) to suggest that a time conflict would exist between mate guarding and extrapair behaviour, because of the costs of doing them simultaneously, something that has been confirmed and documented in many species (Birkhead & Møller 1992). Males are expected to change from mate guarding to the alternative reproductive tactic when their paternity is not at risk and while parental care is reduced, that is during female incubation (Westneat et al. 1990). However, the costs of extrapair behaviour could be lower at high densities of nesting birds, as males might then more easily monitor and gain access to neighbouring females.

Several factors may influence the intensity of mate-guarding behaviour. This is expected to reflect the levels of sexual competition and extrapair paternity present in populations, since high levels of extrapair paternity constitute stronger selective pressures over mated males to defend their paternity, even if extrapair paternity appears to be mostly under female control (Petrie & Kempenaers 1998).

One of the factors considered to have a considerable influence over the intensity of sperm competition is breeding density (Møller & Birkhead 1993; Wagner 1997), since greater proximity facilitates extrapair behaviour. Several studies have found a positive correlation between breeding density and rate of extrapair fertilization (Gowaty & Bridges 1991; Hill et al. 1994; Hasselquist et al. 1995; Westneat & Sherman 1997; Møller & Ninni 1998; Krokene & Lifjeld 2000; Richardson & Burke 2001). Serins

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breed in a semicolonial pattern, with high densities of nests and frequent interactions between pairs (Mota 1995), and so are a good species to study the influence of breeding density on the intensity of sperm competition.

We analysed whether (1) males perform mate guarding, (2) there is a high level of extrapair activity, (3) there is a conflict between mate guarding and extrapair behaviour, (4) the intensity of sexual competition is related to the density of breeding pairs, and (5) extrapair activity is reflected in extrapair paternity.

METHODS

The serin is a nonterritorial cardueline finch that tends to nest semicolonially, a common characteristic of this group of birds (Newton 1972). Estimates based on a nearest-neighbour analysis indicate that serin nests are more than three times closer than expected by a random distribution (Mota 1995). The opportunities for extrapair fertilizations are potentially high because of the absence of territory defence and the close proximity of nests.

We carried out the study in an area close to the Natural Reserve of Paúl de Arzila, near Coimbra, Portugal. The area comprised 50 ha of cultivated fields, with orchards and olive trees, *Olea europaea*, interspersed with oaks, *Quercus* sp., cork oaks, *Quercus suber*, and shrubs, and partially surrounded by pinewood, *Pinus pinaster*. We observed pairs between March and July 1991–1993, from after sunrise (0700 hours) to about 1300 hours. Birds were colour ringed with unique combinations of colours. However, since the population was large and the birds extremely mobile, with new breeders arriving from adjacent areas, only some of the breeding birds were ringed at any time. When the focal birds were not ringed, we used their behaviour relative to the nest and the variations in pattern and intensity of male coloration as forms of identification. We estimated that about half of the breeding males and slightly fewer females were ringed.

We made 146 h of focal-pair observations, of 26 breeding pairs of known laying date. After finding active nests, we inspected them every 2 days to determine the start of egg laying. For pairs with more than one breeding attempt recorded, only the first was considered for the analyses. When both birds were not ringed, we considered only pairs breeding simultaneously, to avoid any possibility of resampling. Focal observations were initiated when at least one member of the pair could be observed and were interrupted whenever contact with the pair was lost. Both members of the pair were followed in the area surrounding the nest, as it is easy to lose contact when birds fly long distances, a relatively common occurrence.

Observation periods lasted 60 min or until the pair was absent for more than 20 min Periods of observation shorter than 10 min were excluded from the analysis. On any given day, we observed pairs in a random order. For each minute of the focal observations we recorded the following behaviours. All behaviours were expressed as rates in relation to the time the female, the male or both were visible in that observation period. (1) Intrapair distance: the distance (5-m intervals) between the two members of the pair. An arbitrary value of 100 m was attributed when the members of the pair were more then 50 m apart, to simplify recording and analysis, since birds fly considerable distances during the fertile period. (2) Movements initiated: we recorded all movements of more than 20 m initiated by one member of the pair and the initiator of the movement. (3) Movements followed: movements initiated by one member of the pair that were followed by the other within 10 s. (4) Copulation: we recorded all instances of within-pair copulations, and whether cloacal contact was achieved. (5) Extrapair copulation attempt (EPCA): one or more males attempted to copulate with a female with which they were not mated. Extrapair courtships, when the extrapair male (EP-male) sang and courted the female with open wings pointing downwards or fluffing the feathers (Mota 1995), were also recorded. (6) Approaches: when one or more males approached the focal female, or the focal male or both. The approaching distance varied with the local visibility and the behaviour of the approaching male and the pair. (7) Chases: directed to the female by one or more EP-males. (8) Male defences: all attacks and chases of EP-males by the paired male. To measure local male abundance for each nest, we defined a circle of 200 m around each nest where we counted the nests and their breeding status. A 200-m radius was considered a good range, since birds travel further than this every day to look for food.

The duration of the fertile period in the serin is not known, so we used a conservative measure by assuming that the female was fertile from 5 days before laying (Birkhead 1988; day -5; day 0 is the day when the first egg is laid) until the third egg of a clutch of four was laid (day $+2$), even though the last behaviourally relevant day is day $+1$, since the last egg is, in principle, fertilized early on day $+2$. In most monogamous passerine birds, however, fertilization is more likely immediately before the start of egg laying. Both within- and extrapair copulations (EPC) long before the start of egg laying are devalued by those occurring closer to it, resulting in the phenomenon of second-male sperm precedence (Birkhead 1998). This is due to passive sperm loss (Birkhead & Biggins 1998) and to the pattern of egg fertilization: each egg is fertilized on each day, about 24 h before laying (observed clutch size variation 3–5). Thus, for the purpose of the analyses, we divided observations into three periods of equal duration, based on the likelihood of fertilization: prepeak fertility (days -5 to -3), peak fertility (days -2 to 0) and postpeak fertility (days $+1$ to $+3$).

Statistical Analysis

To analyse the rate of behavioural variation over the three periods in relation to the female cycle considered above, we used a repeated-measures nonparametric Friedman two-way ANOVA, over 16 pairs sampled in each period, to account for pair resampling. Post hoc tests were a modified Tukey test, following Daniel (1990). All comparisons between pairs were also based on these 16 pairs. A single mean value was calculated for each pair. All probability values are two tailed.

DNA Fingerprinting

Blood samples, drawn from the brachial vein (40–100 µl), were collected from adults ($N=44$) and all ($N=61$) 7–9-day-old chicks, suspended in 0.5 ml EDTA-buffer (10 mM EDTA, 13.4 mM Tris, 0.15 M NaCl) and stored at $-20°C$. Our DNA fingerprinting procedures followed Epplen & Zischler (1990). DNA was digested in the presence of HAE III enzyme, separated by agarose gel electrophoresis at 40 V for 32 h, transferred to a nylon membrane by Southern Blotting and hybridized with a dig-11-UTP-labelled oligonucleotide $(GATA)_4$ probe. We scored a mean $\pm$ SD of 21 ± 2.1 ($N=105$) bands in the approximate size range of 3.0–23 kb to reveal parentage. For each family we assessed the proportion of band sharing between the adults and between putative mother–young and putative father–young, respectively. For each young we also measured the number of novel bands (bands found in nestlings' DNA profile but not found in the DNA profile of putative parents). We followed the method of Westneat (1993a) to set a statistical limit to the number of novel bands arising from mutations or scoring errors and to set 99% confidence limits to band sharing between parents and offspring. The estimated probability of finding one novel fragment per individual was 0.03. Thus, the probability of finding two novel fragments was 0.001 and three novel fragments 1×10^{-6}. Hence, for 61 nestlings, the expected number of individuals with two or three novel fragments was 0.061 and 6.1×10^{-5}, respectively.

RESULTS

Copulation Behaviour and Mate Guarding

Copulation behaviour of pairs was frequent but not conspicuous. We recorded 155 copulations, about half of which occurred between days -2 and 0 (Fig. 1). Copulation rate was highest on day -1 with 2.99 copulations/h. Copulations were significantly more frequent during the peak fertility period (Table 1). Copulation rate did not vary significantly with time (0700–1400 hours; Kruskal–Wallis ANOVA: $H_6=7.137$, $P=0.3$), but tended to peak at mid-morning (1100 hours). No copulations were observed between 1300 and 1500 hours. We did not attempt to record copulations for the rest of the day, but assuming they were concentrated in the morning, we estimated conservatively that a pair copulated 82.1 times for each clutch. From 141 copulations for which male and female behaviours could be precisely determined, 79.4% (112) were solicited by the female.

The mean distance between pair members was lowest during the peak fertility period (Fig. 2a), and increased considerably afterwards. The variation was significant (Table 1), although there was no significant difference between the prepeak and peak fertility periods. Females initiated movements more often during the prepeak fertility period but again there was no significant difference between this period and the peak fertility period. A considerable proportion of female movements were followed by the male, particularly when fertilization was
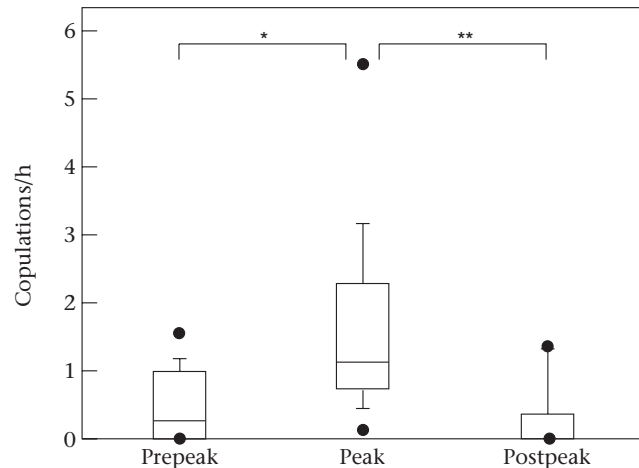

Figure 1. Within-pair copulations of 16 pairs in three periods: prepeak fertility, peak fertility and postpeak fertility. In the box plots, boxes indicate the 25th and 75th percentiles, the line in the box marks the median, whiskers indicate 10th and 90th percentiles and the circles indicate the 5th and 95th percentiles. Horizontal lines at top represent significant differences between categories (post hoc Tukey test: *$P<0.05$; **$P<0.01$).

more likely (Fig. 2b). The variation between the three periods was significant (Table 1). Movements followed during the peak fertility period were also significantly more frequent then either before or afterwards. Thus, intense mate guarding lasted for a short period. There was no significant variation in male movements followed by the female, which were comparatively rare (Fig. 2b). Some males guarded more than others, since there was an almost significant difference in intrapair distance between pairs (Friedman two-way ANOVA: $F_{15,99}=1.749$, $P=0.056$), and the intrapair distance was not significantly correlated with the female-initiated movements (Spearman correlation: $r_S=0.112$, $N=16$, $P>0.2$), suggesting that there is no direct relation between female movements and the intensity of mate guarding.

Intensity of Competition for Fertilization

During all nest-building and laying periods, females were followed and chased by extrapair males that persistently tried to copulate with them. The paired males spent considerable time and energy attacking and chasing other males, trying to keep them away from their mates. The number of extrapair approaches to the females varied significantly over the three periods (Fig. 3a, Table 1), but there was no difference between the prepeak and peak fertility periods. The frequency of approaches to the females was high through most of the fertile period. The number of approaches decreased considerably after the start of egg laying, suggesting that males adjusted their approaches in relation to the female's fertile period.

The number of multimale approaches was higher in the days immediately before egg laying (particularly on days -2 and -1), with an increase in harassment of the female. Most approaches were successfully defended by the mate, and the proportion of defended approaches

Table 1. Repeated-measures nonparametric Friedman two-way ANOVA ($N=16$ pairs) on variation in rates of behaviour in relation to the female's breeding cycle: (1) prepeak fertility (2) peak fertility and (3) postpeak fertility

Behaviour	χ^2_{15}	P	Periods		
			1–2	1–3	2–3
Copulations	13.29	0.001	0.05	0.01	
Intrapair distance	25.13	0.0001		0.01	0.01
Female movements	24.88	0.0001		0.01	0.01
Female movements followed	15.84	0.0001	0.05		0.01
Male movements	16.63	0.001		0.01	0.01
Male movements followed	2.04	0.39			
Extrapair male approaches female	18.00	0.0001		0.01	0.01
Chases of female	11.56	0.002			0.05
Extrapair copulation attempts	8.71	0.01			

Post hoc comparisons between groups were made with a Tukey test.

reached almost 100% on days -2 and -1. Although most approaches were defended by the male, there were still many he was unable to defend. In many cases females were persistently chased by one or more extrapair males. These chases varied significantly between the three periods, and were significantly more frequent in the peak than in the postpeak period (Table 1, Fig. 3b).

Extrapair males often attempted to copulate with paired females. We recorded 52 extrapair copulation attempts (EPCA) directed to mated females by other males. None of them was successful. Some of these attempts included more than one attempt by the same male. EPCAs varied significantly between the three periods, but no significant difference between any two periods was found (Table 1, Fig. 3b). Most EPCA occurred when the female flew to the nest (63.4%; 33/52). Extrapair males often followed females carrying nest material
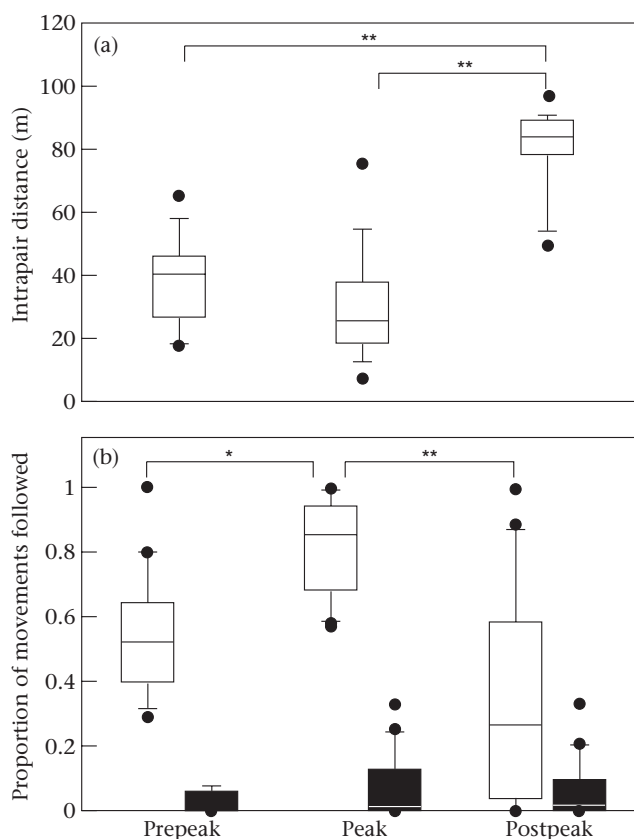

Figure 2. Variation in (a) intrapair distance between mates, and (b) proportion of movements of females (□) and males (■) followed by their mate, in three periods: prepeak fertility, peak fertility and postpeak fertility. See Fig. 1 for other details.
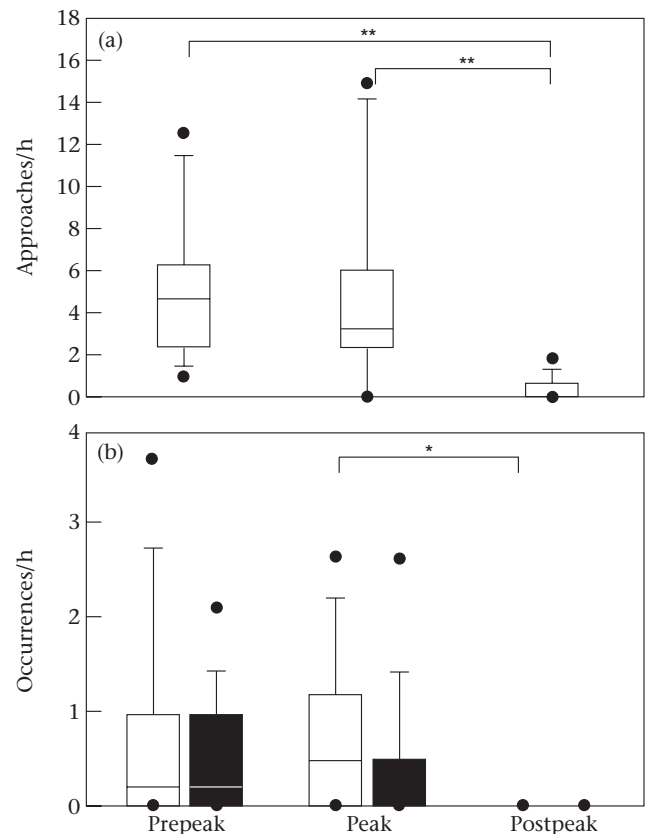

Figure 3. Intensity of harassment of females by extrapair males (a) approach rate to female, and (b) number of chases/h (□), and the rate of extrapair copulation attempts (■) directed to females, in three periods: prepeak fertility, peak fertility and postpeak fertility. See Fig. 1 for other details.
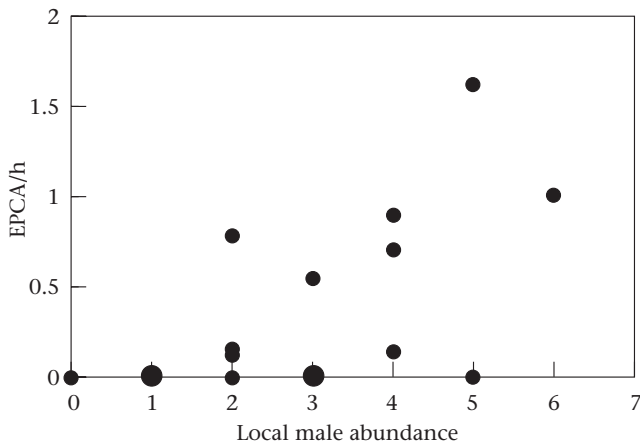
Figure 4. Intensity of extrapair copulation attempts (EPCA) in relation to local male abundance, measured as the number of nests where females were incubating, in a 200-m radius around the focal nest, during the focal female's fertile period. Larger circles represent two cases each.

in their bill. However, females that built more actively did not suffer more EPCAs ($r_S = -0.22$, $N=16$, $P=0.42$).

The amount of extrapair behaviour directed to females varied significantly between pairs ($F_{15,99}=2.199$, $P=0.012$). This was not due to differences in mate guarding, since mate guarding was not correlated with EPCA ($r_S=0.353$, $N=16$, $P=0.18$) or female chases ($r_S=0.265$, $N=16$, $P=0.32$) between pairs. We investigated whether breeding density could be responsible for this variation. Thus, we considered the number of nests where females were incubating, in a 200-m radius around the focal nest, as a measure of local male abundance, assuming that the mates of incubating females were more free to pursue extrapair activities. The frequency of EPCA was significantly correlated with local male abundance ($r_S=0.566$, $N=16$, $P=0.022$; Fig. 4), indicating that breeding density is partly responsible for the variation in extrapair behaviour directed to females.

Of all EPCA observed, we could determine the identity of the extrapair male in 25 cases. In 17 of these the breeding status of the social mates of the extrapair males was known. In five cases (29.4%) these mates were not fertile (four were incubating and one had nestlings) and in 12 cases (70.6%) they were fertile (although only four occurred during their peak fertility period). However, six attempts in the fertile period occurred close to the nest of the extrapair male and were directed to neighbouring females.

Paternity

Our DNA-fingerprinting analysis revealed no cases of extrapair fertilization in the population, in spite of the intense extrapair behaviour of males observed. All 61 young from 21 nests were related to the attending parents. The mean band sharing between putative unrelated adults ± SD was 0.36 ± 0.06 ($N=28$, upper 99% confidence limit 0.51). Band sharing between putative parents and offspring averaged 0.62 ± 0.05 ($N=85$, lower

99% confidence limit 0.52). In spite of our results it is possible that some extrapair paternity (EPP) existed in the population but was not detected because of our small sample size. An estimation of the likelihood of the existence of EPP in this population made through a binomial probability distribution indicates that for an assumed 10% EPP in the population, the probability of observing no EPP in 61 chicks is only 0.0016. That probability drops to 1.23×10^{-6} for a 20% EPP. Even for a 5% EPP the probability of our result is low (0.04). It is, thus, improbable that EPP in the population is as high as 10%. Adjusting our estimate based on the number of broods, the probability of observing no EPP in 21 nests for an assumed 20% EPP in the population is <0.01, and for a 10% EPP 0.1. Values of EPP measured by number of chicks and number of broods are highly correlated in bird taxa (Hasselquist & Sherman 2001).

DISCUSSION

The copulation rate in serins was high, and males guarded their mates intensely, although for a short, but important, period of time. Copulation frequency in the serin is high for a passerine bird (Birkhead & Møller 1992; e.g. 21.8 per clutch, red-winged blackbird, *Agelaius phoeniceus*: Westneat 1993a; 12 per clutch, zebra finch, *Taeniopygia guttata*: Birkhead et al. 1988; 40–120 per clutch, house sparrow, *Passer domesticus*: Møller & Birkhead 1992; 207 per clutch, chaffinch, *Fringilla coelebs*: Sheldon 1992; 250 per clutch, alpine accentor; *Prunella collaris*: Davies et al. 1996). The high copulation rate and its distribution through the fertile period, with most copulations at the end of the fertile period when fertilization is most likely (Lifjeld et al. 1997), are part of a paternity assurance strategy. Males following their mates during the fertile period is in accordance with the mate-guarding hypothesis. Males became involved in extrapair activities, often attempting to copulate with neighbouring females or more distant ones, both during their mate's fertile period and outside it. However, in spite of all this activity, no extrapair paternity was found in the population. This raises two questions: (1) is the absence of extrapair paternity a consequence of female behaviour or of the effectiveness of male paternity guards; (2) why do males devote so much time and effort to extrapair copulation behaviour when it apparently does not pay off?

Extrapair Behaviour

We found that extrapair behaviour was frequent in this species, but, in almost every case, females were unwilling to accept EPCs, often fleeing or alarm calling for their mates, and sometimes even attacking the extrapair male. However, this does not mean that other attempts are equally unsuccessful in achieving insemination and fertilization, particularly if they occur away from the nest and the mate.

The variation between pairs in the incidence of EPCA was most probably due to differences in local breeding density, as there was a significant correlation between the two. The importance of breeding density in extrapair

behaviour and paternity in birds has now been demonstrated in several studies (Hill et al. 1994; Westneat & Sherman 1997; Møller & Ninni 1998; Krokene & Lifjeld 2000; Richardson & Burke 2001).

Male serins attempted to obtain EPCs not only when their mates were no longer fertile, but also when they were still fertile and while males were also involved in mate guarding. The semicoloniality of this species favours these occurrences. A trade-off between the alternative reproductive tactics for paired males in species with paternal care (Trivers 1972) would result in the two tactics being separated in time (Westneat et al. 1990; Birkhead & Møller 1992). Our results indicate that if there is a trade-off between guarding and looking for extrapair copulations in the serin, it is probably less important than in other species.

Extrapair Paternity

We now know that the observed incidence of extrapair copulations is not a good predictor of extrapair paternity (Møller & Ninni 1998), because of both the behaviour of females and possibly cryptic female choice (Westneat 1992; Lifjeld et al. 1993; Dixon et al. 1994; Sheldon & Burke 1994; Eberhard 1996). We expected, though, that EPP ought to be frequent in serins, since males seem to invest so much on extrapair behaviour, although we did not observe females accepting or seeking EPCs. Contrary to these expectations we found no EPP in this population. However, Hoi-Leitner et al. (1999) recorded 19.2% of nests with EPP, in a study of a population of serins from southern Spain. Within-species variation in the levels of EPP has been reported in other species (Gyllensten et al. 1990; Lifjeld et al. 1991; Gelter & Tegelström 1992; Fridolfsson et al. 1997; Gray 1997).

The lack of EPP, despite ample opportunities, suggests that females do not obtain genetic benefits from EPCs. Behavioural observations also show that females can successfully resist EPCAs. There are several possible reasons for the absence of EPP in this population, in spite of the intense extrapair behaviour of males.

Is the absence of EPP a consequence of female behaviour?

One possibility (1) is that there is little variation in male traits related to quality or viability, rendering it difficult for females to make a quick assessment of extrapair males. Although we cannot exclude this possibility, we consider it unlikely, as male coloration, a sexually dimorphic trait, varies considerably in our population (Mota 1995). The absence of EPP could also be caused by (2) an advantage of the mate's sperm and the timing of insemination. This could explain the absence of EPP even with low levels of EPCs, but not why females systematically refuse EPCAs. Females could refuse EPCs because (3) of the risks of being hurt and egg damage from multiple-male EPCs. Nevertheless, they were often approached by single extrapair males and still refused EPCs.

Another possibility (4) is that females may incur high costs if they are involved in extrapair activities, because their mates decrease their paternal care. There is evidence that EPP is negatively related to the amount of male parental investment both within and between species (Møller 2000). Møller proposed that in species where male parental care is important, females choose mates based on direct fitness benefits and do not look for EPCs. Male serins share a considerable amount of parental care with their social mates. They provide courtship feeding during nest building, feed their mates when they have eggs or young nestlings and feed nestlings and fledglings (Mota 1995; Hoi-Leitner et al. 1999). It is certainly important for females to ensure their mate's continued investment. However, this is not an easy hypothesis to test because of possible confounding variables and eventual adjustments of male and female behaviour.

Another possibility (5) is that females accept some EPCs as a fertility insurance function, to compensate for possible low male fertility in the population. If there is a significant risk of male infertility, and EPCs are generally costly to females, they could accept only one or a few insurance copulations with extrapair males. As a result, most nests would contain no EPP because of the numerical dominance of the within-pair copulations. But in those few cases where the male is functionally infertile, the entire brood should be sired extrapair. If most females perform a few insurance EPCs, then sperm competition will drive the evolution of male paternity guards. There will also be a premium on males to pursue EPCs, because when they are eventually successful they may father an entire clutch (if the social mate is infertile) or at least a few nestlings. This leads to the predictions that a significant proportion of males in the population are infertile, and that some clutches would be sired entirely by a single extrapair male. If there is considerable population variation in male infertility, then female behaviour should adjust to it with more EPCs where infertility is higher. Infertility should not be caused by inbreeding in large populations with female dispersal, but by other, possibly external, environmental fertility suppressors. So far, we can only say that in our study putative fathers were determined by behavioural observations and there were no exclusions of their paternity, while levels of band sharing with young were similar between males and females.

Why do males devote so much effort to EPC behaviour?

It is not clear why males should devote so much time and effort to attempt EPCs if they do not seem to be successful. One hypothesis is that females occasionally accept EPCs which would be sufficient to maintain the alternative male tactic in the population. This could be a consequence of a fertility assurance strategy by females to reduce risks of infertility, so that the occasional EPP compensates males for the costs of attempting EPCs.

Another hypothesis is that male extrapair behaviour is not competing with other male activities at times when their mates are incubating. During that period males are free from mate guarding, while they do not have to maintain a territory, leaving plenty of time for extrapair behaviour, even though it does not often lead to EPP. The costs are low since there are no conflicting activities. It

remains to be determined how low EPP can be and still compensate for the costs of engaging in extrapair behaviour.

A third hypothesis is that, in our population, female costs for EPCs are high because of a possible reduction in male parental care, so that few or no EPCs occur. But because the importance of this constraint on females is not determinable by males, they maintain the extrapair activity that sometimes leads to EPP. This would agree with Hoi-Leitner et al.'s (1999) results.

Further analysis of the costs and benefits for males and females of mate guarding and extrapair behaviour are needed to understand how a species can reveal such high levels of sexual competition with little or no genetic polyandry.

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